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Some Eocene leaf fragments comparable to Proteaceae.

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Abstract

Six hundred Eocene leaf fragments from Australian deposits were compared with four thousand small fragments arbitrarily drawn from Australian region perennial angiosperms, to examine similarities between Eocene and living forms. Various instances of similarity were detected and those involving Proteaceae were examined in detail. Four fossils are described. One from Western Australia resembles *Synaphea* and the others, from South Australia, include evidence for *Darlingia*. The evaluation of their evidence and the ascription of the fossils to living taxa are discussed in relation to the circumspection evident about both issues in Australian literature.

Introduction

In Australian Tertiary deposits there are many strata that contain carbonaceous fossil angiosperm leaves. Where they outcrop or are exposed by quarrying the long-established study of whole-leaf and shoot compressions may proceed, but for every leaf-bearing stratum that outcrops in South Australia for example, perhaps a hundred others are known only from drill cores which yield only fragments not whole leaves. The question arises as to what palaeontological evaluations can be made of the evidence presented by such fragments.

Three viewpoints seem relevant. First, the fragments can be scanned for fossil epiphyllous microfungi (Felix 1894, Edwards 1923, Cookson 1947, Dilcher 1965, Lange 1969, 1976, Selkirk 1972, 1975). In this regard fragments are little less informative than whole leaves, and so have the advantage of permitting access to epiphyllous microflora in drill-core samples.

Second, the fragments have been studied with a view to developing catalogues and classifications of their variety, without reference to the taxonomy of living angiosperms, to assist correlation (Arbeitsgruppe Cuticulae 1964, Meyen 1966, Lange 1969b). Little progress with this approach is evident in Australia.

A third possible viewpoint is that the fragments might be amenable in some degree to the same approach used on whole-leaf compressions, i.e.—to arguments that their source plants were or might have been relatives of particular living angiosperm taxa. This is a difficult viewpoint to maintain. First, it appeals to similarity between living and fossil leaves as demonstration that they are of the one stock whereas ancestral leaves must involve dissimilarities with descendants. Further, ascription of fossils to living taxa is justified scientifically only when it contributes to rigorous accounts of their prehistory, evolution and phylogeny but evidence is that the fossil angiosperm literature has a poor Australian acceptance in that regard. Thus a substantial literature about fossil *Eucalyptus* is ignored by Johnson (1972) and is described by Carr and Carr (1969) as ". . . utterly inadequate." while that dealing with fossil Proteaceae is criticized for its erroneous claims (Johnson and Briggs 1963) and is described as ". . the absence of a useful fossil record" (Johnson and Briggs 1975). There is no reason to believe that deductions based on leaf-fragments will be better received.

On the other hand no Australian investigation seems to have been reported on the potentials and limitations of the approach as it applies to dispersed Tertiary leaf fragments, and to dismiss it out of hand is to risk ignoring substantial evidence about the prehistory of some taxa, perhaps the only fossil evidence. The present study therefore takes up the question on the basis of crossmatching between 600 Eocene fossil fragments and 4 000 fragments representing a wide range of living perennial angiosperms from the Australian region.

For the great majority of the fossils, no matches of a provocative, exclusive nature were detected. In a small minority of cases, fossils resembled the representatives of a particular living taxon in the 4 000-fragment sample and were dissimilar to all the others. Cases involving Proteaceae were selected for an evaluation which is reported here.

First a detailed acquaintance with leaf cuticles of Proteaceae was gained from a specially assembled slide collection, then the fossil leaf fragments were individually examined for close similarity with living Proteaceae. Four of the matches are described and discussed with regard to the evidence they provide. The issue of their ascription to Proteaceae is then considered.

Materials and methods

The source sediments of the fossils described were carbonaceous clays from Lake Lefroy, Western Australia (University of Western Australia Geology Department sample 76768 Lake Lefroy WMC KD 3009A 50m) supplied by D. Hos of the South Australian Mines Department,

who determined its palynological age as late Eocene, and from Maslin Bay, South Australia (Lange 1970), determined as early Middle Eocene by McGowran, Harris and Lindsay (1970). Others from which fragments were recovered were from Golden Grove, South Australia and Anglesea Power Station, Victoria, both considered on the basis of unpublished palynological studies to be of Eocene age (W. Harris, pers. comm., Dec. 1976).

Samples digested in Schultz solution yielded small chips of leaf from which the cuticles, freed by dilute KOH solution, were mounted unstained in phenol glycerine jelly. Cuticles from living plants were prepared similarly (Lange 1976). Phase contrast and Nomarski interference phase contrast microscopy were used to study them. Because the coloured images of Nomarski observation yield poor monochrome photographs, the latter were supplemented with drawings. To extend comparisons with Proteaceae, cuticle slides were prepared from herbarium specimens including many kindly supplied by Dr. L. A. Johnson of the National Herbarium of New South Wales who with Dr. Briggs has provided the major account of the evolution and classification of the family (Johnson and Briggs 1975). This included slides from Proteaceae ascribed to *Adenanthos, Agastachys, Banksia, Bellendena, Buckinghamia, Cardwellia, Cenarrhenes, Champereia, Conospermum, Darlingia, Diastella, Dryandra, Embothrium, Fauria, Finschia, Franklandia, Grevillea, Hakea, Helicia, Hicksbeachia, Isopogon, Kermadecia, Knightia, Lambertia, Leucospermum, Lomatia, Macadamia, Oreocallis, Orites, Petrophile, Persoonia, Protea, Roupala, Serruria, Stenocarpus, Stirlingia, Strangea, Symphionema, Synaphea, Telopea and Xylomelum.*

Descriptions of the fossils

Lake Lefroy cf. Proteaceae I

Slide Lake Lefroy cf. Proteaceae I, Adelaide University Botany Department, see Figs. 1-16. The fragment consisted of a 5 mm length embracing a central straight rib with torn lateral fringes of blade and was bifacial with dissimilar surfaces. The cuticle of the stomatiferous surface is thin and fragile relative to that of the non-stomatiferous which is thick and robust. Outlines express venation on both cuticles, pronounced on the stomatiferous where it is associated with contrasting cell outlines and subdued on the reverse where one type of cell extends over veins and between them.

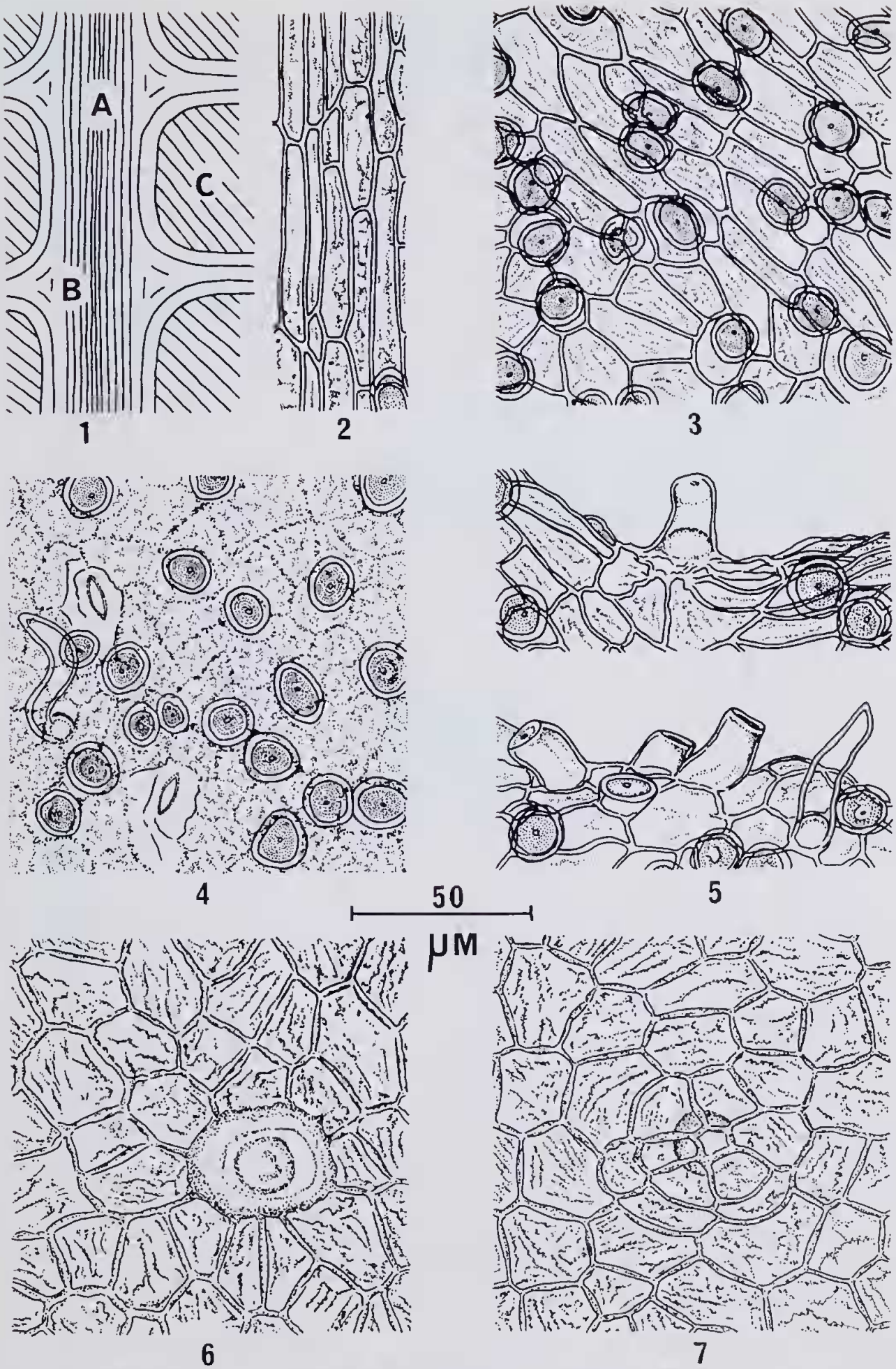
Figure 1 is a zone-diagram of the stomatiferous cuticle. Lateral veins about 80 μm wide leave the main vein at right angles at intervals of about four times their breadth and are approximately opposite. Central cell outlines of the main vein (zone A) are straight, narrow, about 5 x 55 μm in most cases and strictly parallel along the rib. Infrequent small cells bear a stubby papilla up to 25 μm long. Each is cylindrical truncate and rounded off not torn at the summit (Figs. 5, 14). The trend of cell long axis along the rib is less strict at its margins (zone B, Figs. 3, 11). Outlines are relatively broader and shorter and some are compact polygonal. There are more small outlines with the papilla, about 1 500-2 000/mm^2 of leaf surface. In the transition between main and lateral venation the trends of cell long axis orientation are as shown in the zone diagram.

Cuticle of the leaf blade between lateral veins (zone C) contrasts with the rest. Cell wall traces are fainter, are compact polygonal and have no trend of orientation (Figs. 4, 12, 13). Most of the smaller cells bear the same papilla as in zone B but some carry a simple, unicellular hairshaft 40-50 μm long (Figs. 4, 5, 14, 16). It may be curved or nearly straight, has thick unornamented walls and is acute (Fig. 16). Scattered in zone C are stomatal traces which are difficult to see and relatively sparse. Each consists of a thin, translucent area of cuticle with a delicate narrow elliptical slit-like trace about 3 x 12 μm in its centre (Figs. 4, 12, 13). They have no particular orientation, and appear to be anomocytic.

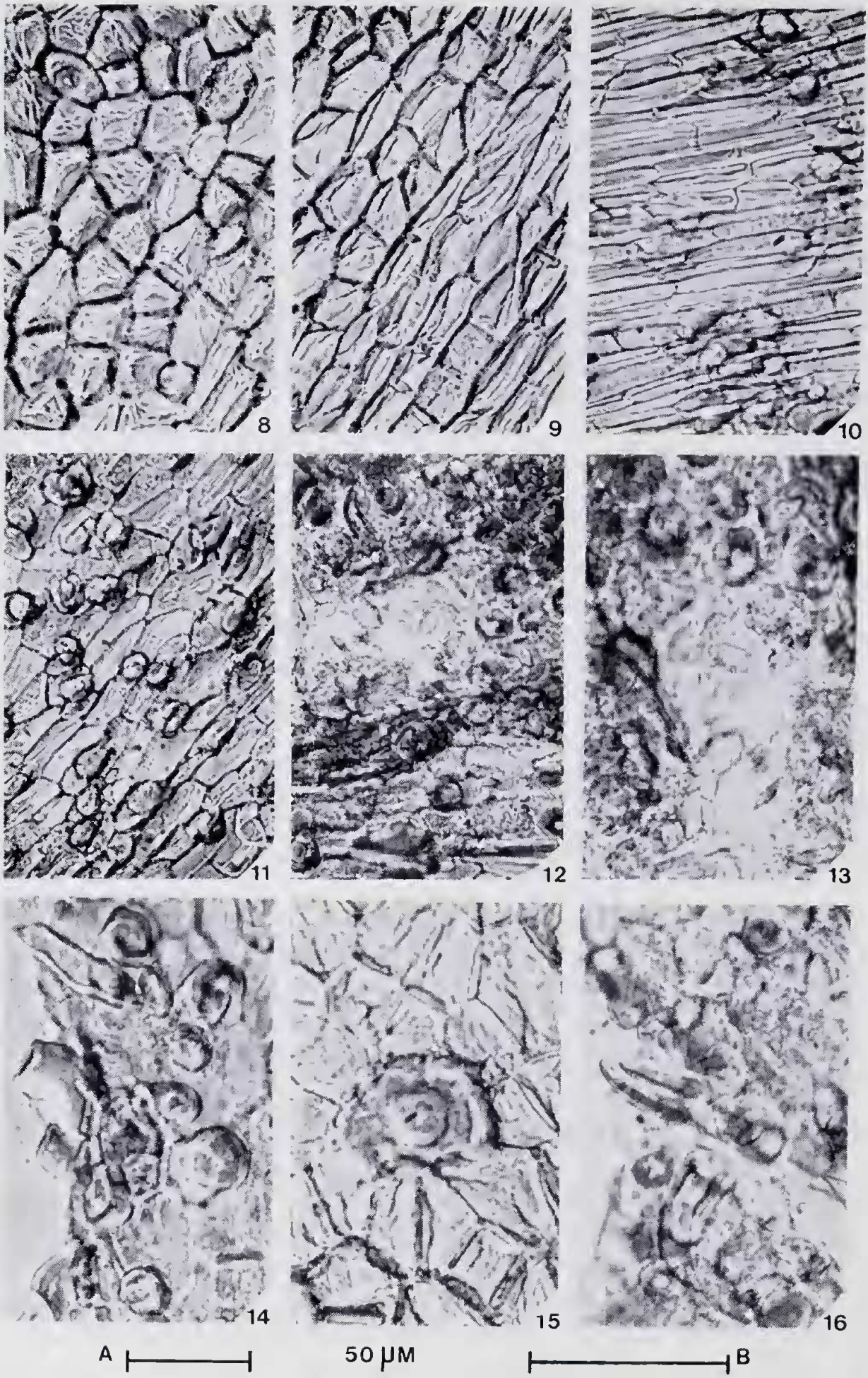
On the non-stomatiferous surface cell outlines are robust compact polygons with maximum dimension about 40 μm (Figs. 6, 8, 15). Those over veins tend to be elongate (Fig. 9). The cuticle within each outline shows a characteristic appearance of crease lines (Figs. 8, 15). Scattered sparsely are rounded polygonal cells each bearing a distinct, circular disc-like scar like that of a deciduous hair (Figs. 6, 8, 15). In no case does the scar lap the cell boundary. A further structure of which only one example was found consists of a group of cells of which the shared walls converge radially to a common fused centrum (Fig. 7). Cuticles of both surfaces have fine creasings and granulations which, like the appearance of the wall outlines themselves, defy ready terminology (Figs. 8, 11, 12).

Maslin Bay cf. Proteaceae II

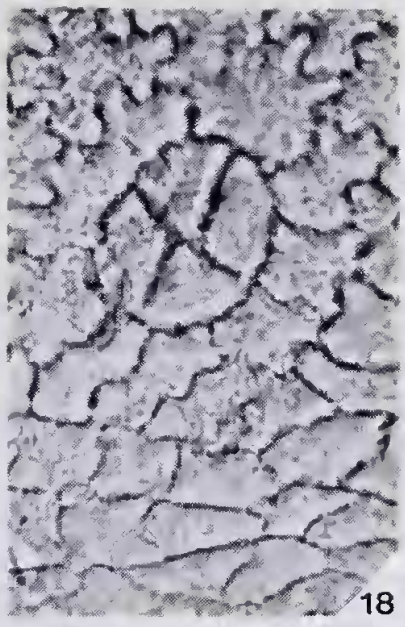
Slides Maslin Bay cf. Proteaceae II, 1-8, Adelaide University Botany Department, see Figs. 17-19. The largest fragment embraces 1 cm of entire margin. The leaves are bifacial. The non-stomatiferous face is surfaced primarily with the one sort of unoriented cells of maximum dimension 15-35 μm. Walls are sinuous and between junctions have 1.5-2 waves of which the amplitude may approach the wavelengths but usually is less. On and near veins, walls are thinner and straight and outlines elongate. The cuticle lacks striation but has some indiscriminate punctation. The outstanding feature of the non-stomatiferous face is the striking appearance of the many complex hair bases (Figs. 17, 18). Each involves a discrete group of epidermal cells, typically 4-12 and commonly about 8, of which their collective perimeter is circular to ovoid tapered. Cell walls within this perimeter are thicker, straight and tend to meet at right angles with the overall appearance of a grille. Above the grille on the outer surface of the cuticle is the faint but definite scar of a deciduous hair. This scar shows up under interference phase contrast as the inner of two well-separated concentric circles or ovoids which are very finely drawn and lap all or most of the cells in the grille but not their collective

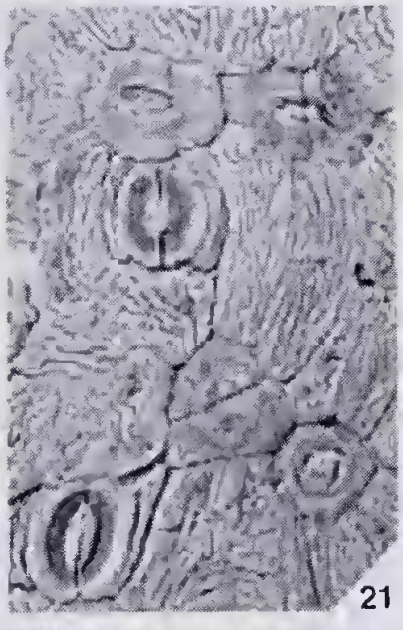


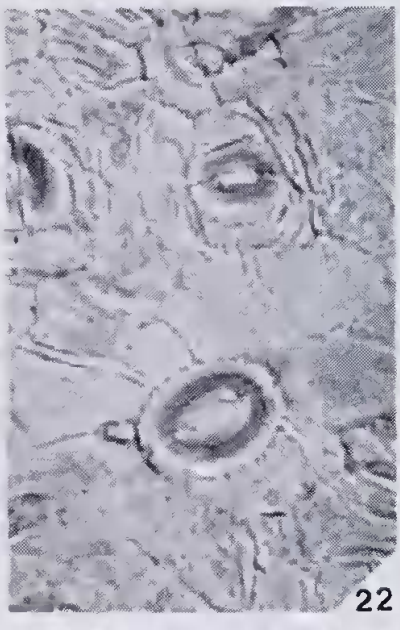
Figures 1 to 7.—Lake Lefroy cf. Proteaceae I. Drawings based on interference phase-contrast microscopy. 1.—Zone-diagram of the stomatiferous surface. 2.—Stomatiferous surface zone A; cell outlines of the central main vein. 3.—Stomatiferous surface zone B; cell outlines at the margin of the main vein; the dark circular outlines are the summits of papillae developed from small underlying cells. 4.—Stomatiferous surface zone C; cell outlines of the stomatiferous areas showing papillae, stomatal traces and a unicellular hair. 5.—Stomatiferous surface; two examples of the cuticle rolled to display trichomes in lateral view. 6.—Non-stomatiferous surface; inter-vein outlines including an example of the occasional cell with a deciduous hair scar. 7.—Non-stomatiferous surface showing the rare structure with walls of a group of cells radially convergent to a centrum.

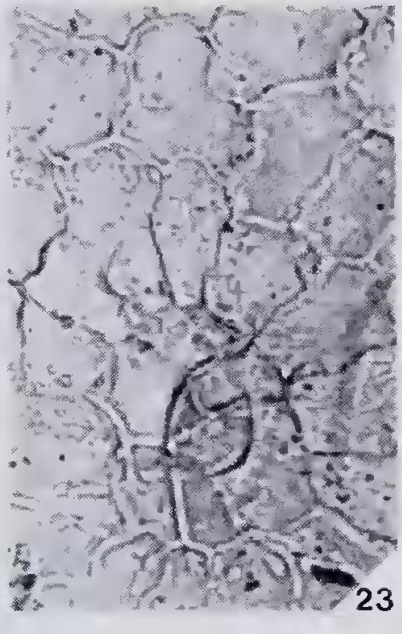


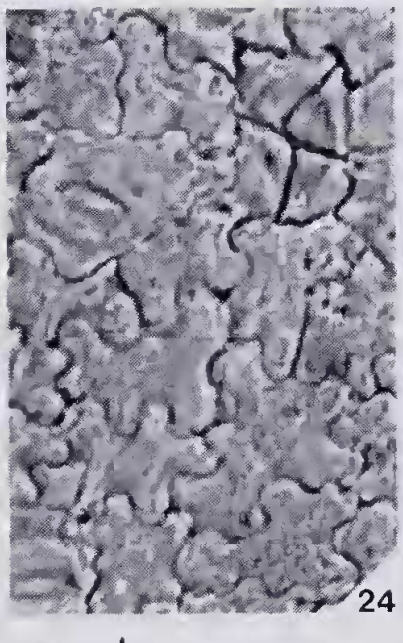
Figures 8 to 16.—Lake Lefroy cf. Proteaceae I. Monochrome photographs of cuticular fields which under interference phase-contrast microscopy involve colour contrasts. Figures 8-12 inclusive, scale A; Figures 13-16 inclusive, scale B. 8.—Non-stomatiferous surface showing the robust polygonal cell wall mesh, the characteristic cuticular creasing and occasional cells with a hair scar. 9.—Non-stomatiferous surface showing elongation of cell outlines over a vein. 10.—Stomatiferous surface showing the narrow parallel outlines of zone A with occasional papillae developed from interspersed short cells. 11.—Stomatiferous surface; cell outlines in zone B. 12 and 13.—Stomatiferous surface showing a stomatal trace both in context and in detail. 14.—Stomatiferous cuticle rolled to show trichomes in lateral vein. 15.—Non-stomatiferous cuticle showing a deciduous hair scar in detail. 16.—Stomatiferous cuticle rolled to show simple unicellular hairs among papillae.

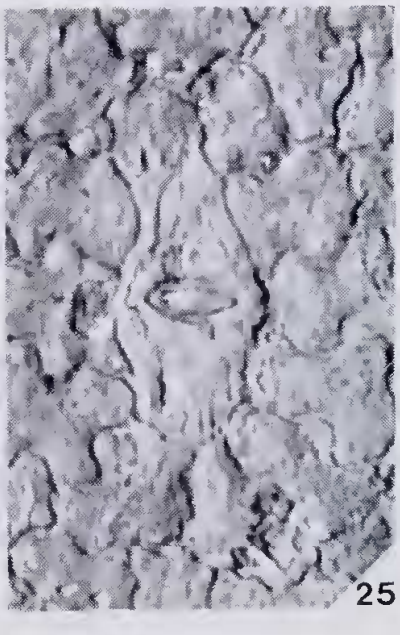












50 µM

'igures 17 to 25.—Monochrome photographs of cuticular fields which under interference phase-contrast microcopy involve colour contrasts. 17 to 19.—Lake Lefroy, cf. Proteaceae II. 17.—Non-stomatiferous surface showing pidermal cell outlines and a complex hair base with overlying scar. 18.—Non stomatiferous surface showing hinner, straighter walls near a vein. 19.—Stomatiferous surface showing stomatal trace, several hair bases nd lengths of wavy wall. 20 to 22.—Lake Lefroy cf. Proteaceae III. 20.—Non-stomatiferous surface showing typical omplex hair base and striae. 21.—Stomatiferous surface showing 1- and 2-celled hair bases, some joined; striae nd stomates. 22.—Stomatiferous surface showing a large stomate with faintly-marked actinocytic surrounds; lso the remains of a hair shaft on a 2-celled base. 23 to 25.—Lake Lefroy cf. Proteaceae IV. 23.—Non-stomaliferous surface showing tangled wall traces and hair base. 24.—Stomatiferous surface showing sinuous walls. omplex hair base and stomata. 25.—Stomatiferous surface; lateral striae about the transverse stomatal slit in an elongated stomatal window.

perimeter. The maximum diameter of perimeters is 40-60 μm. They occur both on and between veins and average about 50/mm². Some are more or less linked by their narrow tapered ends.

The stomatiferous face has much thinner cuticle. Cell wall traces are marked only faintly and in places and fade out particularly near stomates. They are finer than on the reverse face and have up to five small irregular waves between wall junctions. They are most visible over veins where they are more or less straight, outlining elongate, oriented cells. Stomatal traces are extremely faint. Each is a circular to ovoid patch of smooth cuticle about 16 μm across with a central elliptical trace about 6 μm long. They appear anomocytic and unoriented at about 340/mm² (Fig. 19).

Hair bases average about 320/mm² on the stomatiferous face. Each has an outline 10-35 μm across enclosing a creased, more or less circular structure suggesting the attachments of a deciduous hair shaft. Some underlying outlines are unsectored but larger examples are sectored by thin straight walls either parallel, or intersecting at wide angles. On veins, delicate versions of the hair base characteristic of the non-stomatiferous face occur with a distinct ovoid scar overlying the grille. They are oval to elongate up to 35 μm, and some are linked in pairs by their narow ends.

Maslin Bay cf. Proteaceae III

Slides Maslin Bay cf. Proteaceae III, 1-2, Adelaide University Botany Department, see Figs. 20-22. The fragments are bifacial. The non-stomatiferous face is surfaced primarily with uniform polygonal cells of 5-7 angles and maximum dimensions 15-35 μm. Walls vary from slightly crooked to lightly curved, sometimes in a flat sigmoidal curve. In places they fade out. Over expanses up to 0.5 cm², the largest available, there is no variation in cell shape or orientation to suggest veins. The outstanding feature of the non-stomatiferous face is the striking appearance of the many complex hair bases in combination with the bold cuticular striation which runs between them (Fig. 20).

Each base involves a discrete group of cells, from 2-14 but typically 4, of which their collective perimeter is a compact irregular outline 40-80 μm across, sometimes more or less circular to tapered ovoid but with angular indentations at wall junctions. Each base is picked out by the contrast between its smooth cuticle and the intervening cuticular surface which is boldly striate at about 7 parallel striae/cell width, running in unbroken patterns that converge on the smooth bases. Each base is sectored into an angular grille. A large ovoid scar of a deciduous hair is easily seen on the cuticle overlying the grille (Fig. 20). It consists of two concentric circles finely drawn, which lap all or most of the underlying grille cells but not their collective perimeter. Some still carry the hair which is based on the inner of the two circles and has a simple, unicellular, thin-walled shaft without ornament, about 70 μm long.

Cuticle of the stomatiferous face is thinner and primarily surfaced with angular polygonal cells of maximum dimension 20-30 μm in arrangements that tend to be actinocytic upon the numerous hair bases. Wall traces are thin, faint and break up, fading out into granulations; among the striae which are finer, also fade out in places and do not describe the unbroken lines that characterize the reverse surface. They tend to be diffuse with local convergences on hair bases. There are two sizes of stomata which differ in numbers and arrangement but are otherwise similar. Each is enclosed by an oval to subcircular ring of the same fine wall that outlines general epidermal cells. This outline may be notched at the poles. Within this perimeter and separated from it by a band of thin smooth cuticle about 2-3 μm wide is a thick, smooth refractile band, oval in outline and about 4 μm broad. This encloses fine, smooth cuticle with a slit-like trace or crease over the long axis of the stomate. At each pole, projections from the perimeter wall extend inwards on the long axis across the thick band to the edges of the central slit.

Small stomates are scattered without orientation at about 270/mm². They are about 18 μm long and appear paracytic, with narrow curved lateral subsidiary cells, large epidermal cells abutting the poles and no convergent striae. Large stomates about 27 μm long and about 10/mm² are separated from the smaller by surrounds of epidermal cells of which the walls are very indistinct but sufficient to show that the large stomates lack narrow paracytic subsidiaries. Surrounding cells tend to wedge inwards against the stomatal perimeter in actinocytic pattern (Fig. 22).

Scattered among the stomates at about 120/mm² are hair bases. Some involve an angular to ovoid cell outline about 25-30 μm across enclosing the circular, creased base of a hair about 20 μm in diameter. Others involve an angular ovoid perimeter about 30-80 μm across with a single straight crosswall, lapped by the ovoid scar of a deciduous hair. These bases are sometimes joined in pairs by their narrow ends. Some still carry the hair which is a simple, unicellular, thin unornamented shaft about 40 μm long (Fig. 22), inserted on the inner ring of the scar. Less frequently the base consists of an ovoid to lenticular perimeter sectored into a grille of up to 7 or more cells, most of them lapped by the scar. Occasionally 2 or 3 lenticular bases are joined at their narrow ends.

Maslin Bay cf. Proteaceae IV

Slides Maslin Bay cf. Proteaceae IV, 1-7, Adelaide University Botany Department, see Figs. 23-25. The fragments are bifacial and the greatest length of margin represented, 1.5 cm, is entire. The non-stomatiferous face is surfaced with cells about as long as wide and of similar size, about 18-25 μm. Their walls show the enigmatic condition illustrated by Lange (1969b, fig. 10), i.e. they are like cords which loop across each other, tangle, fuse and sometimes show free projecting ends (Fig. 23). Outlines are thus

more or less square to polygonal with erratic sinuosities and looped double strands in places. Over areas up to 1.5 cm^2 (the largest available) the pattern shows no veins. The cuticle is indiscriminately punctuate and in places shows fine striae converging on occasional hair bases.

Hair bases are scattered sparsely at about 10/mm^2. Each involves a group of 2-5 epidermal cells, commonly 4, with a collective perimeter roughly circular, ovoid or lenticular 30-50 μm across. Internal walls describe an untidy sometimes tangled grille. Over the grille is a circular to ovoid hair scar which laps most cells but not the perimeter.

The stomatiferous face has thinner cuticle. It is primarily surfaced with non-oriented uniform cells about 20-40 μm across with fairly regular sinuous outlines. Walls between junctions have 1.5-2 waves of sinuosity of which the amplitude is about half the wavelength (Fig. 4). In places the wall traces loop and tangle. Scattered among the general epidermal cells are stomates, complex hair bases and occasional lesions ringed by a converging pattern of many cells and interpreted as a malformation due to fungal parasitism. The stomates are very characteristic. Each occupies a window of extremely thin, delicate, creased cuticle 25-35 μm across which appears to supplant an ordinary epidermal cell and is highlighted by its translucency relative to surrounding cuticle. Transverse to the long axis of the window is an ellipse about 6-9 x 16-18 μm which is thick walled and encloses a clear central area. In many cases a pattern of creases runs from the sides of the ellipse to the ends of the window (Fig. 25). Stomata occur at about 160/mm^2 and are not oriented.

The hair bases are discrete groups of cells of which the collective perimeter is usually ovoid, up to 55 μm across. Straight walls either transverse, or intersecting at wide angles, describe a grille, above which lies the scar of a deciduous hair.

Comparisons with Proteaceae

Lake Lefroy cf. Proteaceae I

Each cuticular feature of this form finds ready matches among living Proteaceae at least as a clearly-related version of a condition well represented in the family. The same applies to progressive combinations of features, up to the case where the total combination is embraced by a particular living genus, but no single species, of Proteaceae.

When the fossil is compared with cuticles from the range of Proteaceae listed earlier only *Banksia*, *Dryandra* and *Synaphea* appear to accommodate its fundamental combination of characteristics, namely: bifacial leaves with thin stomatiferous and thicker non-stomatiferous cuticles, the non-stomatiferous with only robust polygonal cell outlines, characteristic cuticular wrinkling and occasional cell outlines bearing the distinctive scar of a deciduous hair; lateral venation leaving the main vein at right angles and closely spaced to enclose stomatiferous cuticle into many rounded patches; those patches bearing many trichomes and stomatal traces which consist of thin translucent areas surrounded by thicker cuticle and exhibiting a delicate elliptical slit-like central trace.

Between *Banksia* and *Dryandra* on the one hand and *Synaphea* and the Lake Lefroy fossil on the other, various features discriminate. *Synaphea* and the Lake Lefroy fossil both exhibit papillae and unicellular hairs interspersed. *Banksia* and *Dryandra* do not. They have bicellular hair shafts of a distinctive sort which, so far as is illustrated from fossils (Cookson and Duigan 1950), never break off to leave basal cells at all like the papillae of the Lake Lefroy fossil; instead they leave bases which are torn at the summit. In addition, hair scars on *Synaphea* and on the Lake Lefroy fossil are always contained within one epidermal cell outline whereas on many *Banksia* and *Dryandra* hair scars lap more than one epidermal cell.

Maslin Bay cf. Proteaceae II, III and IV

All cuticular features of each of the three forms find matches among living Proteaceae either as an indistinguishable match, a very close resemblance or as a version of a condition represented in the family. The degree to which progressive combinations of the fossils' characteristics leads to exclusive matches within Proteaceae varies between the three forms. Maslin Bay cf. Proteaceae III has features of which the comparison of progressive combinations eliminates all but *Darlingia* and *Knightia* with the weight of similarity to *Darlingia*, which exhibits the same stomatal appearance in detail, the same variations in stomatal size, the same form of paracytic subsidiaries, the same variability in strength of cell wall trace, similar striae and the same sorts and variety of hair bases on the stomatiferous surface. It differs by having more or less straight walls whereas *Darlingia* has sinuous walls. *Knightia* matches less well, lacking paracytic subsidiaries or variety of stomatal size. The non-stomatiferous surface of the fossil similarly indicates *Darlingia*.

Forms II and IV are not so tractable. The stomatiferous surface of form II indicates *Helicia* in respect of the characteristic hair bases, faint wall traces with many small waves, and round anomocytic stomates in the particular arrangements presented, but reference to the non-stomatal surface while strengthening evidence for Proteaceae, leads away from *Helicia* back towards genera such as *Darlingia*. Form IV is the most intractable. For example its transverse elliptical stomatal slits bisecting translucent cuticular windows and with flanking striae find parallels in *Finschia*, its rather delicate and crumpled complex hair bases in *Helicia*, its tangled net-like wall traces in *Grevillea*, and so on, but a substantial combination of its characters were not found in any of the comparison genera.

Discussion

It was hoped that particular living vegetations might show up as rich matching sources for Australian Eocene fragments, but none did. The probability of a highly-distinctive close match

between arbitrarily-drawn fossil and living fragments (at or near the species level) was very remote ($p < 0.00001$).

It took ten years to accomplish the 2.4 million comparisons involved in this study. This does not encourage the idea that an Australian assemblage of Eocene angiosperm leaf-fragments (too fragmentary to convey leaf macromorphology) is likely to be elucidated as to its botanical affinities with living species simply by making a large number of arbitrary direct comparisons.

Nonetheless instances of distinctive close comparability can be detected by the approach and it is simple if laborious in some cases then to specify that the match is exclusive within certain limits, e.g. to 0.2% of genera in a large random sample of Australian region angiosperms.

If arguments are to be pursued about phyletic relationship between forms thus matched (with ascription of the fossil to the taxon of the living comparison material) the question is whether such demonstration of exclusiveness is adequate. Here the issue is not whether the demonstration convinces the investigator but whether it will convince taxonomic botanists in general and the Australian experience is that the latter expect very rigorous demonstration. Clearly, it would be mere sciolism to ascribe the fossil outright to the first match detected.

Thus in the course of this study, complex hair bases as in Fig. 20 were for a long while observed only from Proteaceae. When seen in leaf-litter samples from widely-scattered vegetations (Lange 1976) back-checking to the source plant invariably led to Proteaceae regardless of whether the litter came from Tasmania, New Zealand or mainland Australia. Subsequently a very similar hairbase was detected from Araliaceae of New Guinea and a related structure from northern hemisphere *Platanus*. Similarly papillae as in Fig. 14, long observed only from Proteaceae, were detected in Barringtoniaceae as comparisons widened.

There seems to be no limit to the comparisons that might be deemed adequate to specify the exclusiveness of a match. The ascription of northern hemisphere Cretaceous fragments to the phyletic lines of living Australian and New Zealand genera (Rüffle 1965) illustrates how cuticular analysts already regard global flora as potential comparison material.

Fossil fragments could not be matched and specified as to their exclusiveness more readily at the family than the species level. Many families tend to be very heterogeneous in cuticular characteristics. Some Proteaceae have nothing cuticular in common with others and instead resemble species in other families.

Essentially, the approach examined in this paper tends to founder on the disproportion between available and necessary comparison data and on the immense work necessary to bridge the gap.

The Western Australian fossil which resembles *Synaphea* provides first indications from leaf-cuticles for the presence in Palaeogene floras of any of the endemic Western Australian Proteoideae, or the subfamily itself. The South Australian fossils include evidence for *Darlingia*, which is very close to *Knightia*. This reintroduces the question of these genera in Palaeogene floras following refutation by Dilcher and Mehrotra (1969) of some earlier claims for *Knightia*.

As matters stand, this evidence must remain at a face value that cannot be upgraded without much wider studies of living angiosperm cuticles. It is strong evidence, but not yet enough to allow ascriptions to the living genera without significant risk of sciolism, or to convince rigorous botanists.

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